Modeling the Size–Density Relationship in Direct-Seeded Slash Pine Stands

Quang V. Cao, Thomas J. Dean, and V. Clark Baldwin, Jr.

ABSTRACT. The relationship between quadratic mean diameter and tree density appeared curvilinear on a log–log scale, based on data from direct-seeded slash pine (*Pinus elliottii* var. *elliottii* Engelm.) stands. The self-thinning trajectory followed a straight line for high tree density levels and then turned away from this line as tree density decreased. A system of equations was developed to model the reciprocal effects of stand diameter and density through time. The equations performed well for these data. Since the model is constrained according to the self-thinning rule, it should provide reasonable extrapolation. For. Sci. 46(3):317–321.

Additional Key Words: *Pinus elliottii*, self-thinning, −3/2 power rule, size-density trajectory.

THE RELATIONSHIP BETWEEN TREE SIZE AND tree spatial density has been a topic of research and discussion for more than six decades. Reineke (1933) found that the maximum quadratic mean diameter at breast height (Q) for a given number of trees per unit area (N) could be represented on a log–log scale as

$$\log (N) = a + b \log (Q). \tag{1}$$

Reineke (1933) reported a slope of −1.605 for 12 out of 14 species examined. Steeper slopes were noted for slash pine and shortleaf pine. For loblolly pine (*Pinus taeda* L.), the slope was estimated to be −1.707 by MacKinney and Chaiken (1935), −1.696 by Harms (1981), and −1.505 by Williams (1996). Bailey (1972) computed a slope of −1.58 for radiata pine (*Pinus radiata* D. Don). Drew and Flewelling (1977) pointed out that the normal densities published for Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) by McArdle et al. (1961) closely followed Equation (1) with a slope of −1.54.

An analogous relationship relating mean size and tree density is the so-called −3/2 power rule of self-thinning (Yoda et al. 1963) that expresses size in terms of biomass or volume. Given a weight-diameter relationship (e.g., Ogawa et al. 1961), the −3/2 power law can be rewritten in the form of Equation (1) with a slope of −1.67 (Drew and Flewelling 1977, White 1981). Both the Reineke equation and the self-thinning rule describe the maximum number of trees that can exist for a given mean size and have been useful in developing mathematical models to describe stand development with time (Smith and Hann 1984, 1986, Lloyd and Harms 1986, Somers and Farrar 1991, Cao 1994).

Current growth models that incorporate the limiting size–density relationship have assumed that the logarithmic form of the relationship is linear throughout the entire range of tree densities. Even if the relationship is curvilinear, as has been shown with data from yield tables (Zeide 1987), this assumption is still valid for either a narrow range of tree densities (interval A), or for a wider range of relatively high tree densities (interval B), as illustrated in Figure 1. As self-thinning proceeds and tree density declines, the trajectory diverges from a linear relationship, approaching a zero slope.

The relationship between the log of quadratic mean diameter and the log of tree spatial density in self-thinning, even-aged monocultures of trees was never considered linear throughout the entire range of tree density because trees are limited in size by their weight, restricting the maximum diameter associated with lower spatial densities (Westoby 1984). Forest management models are unaffected if the departure from linearity occurs below the typical densities of a managed forest. If the departure occurs within typical management densities, mathemati-

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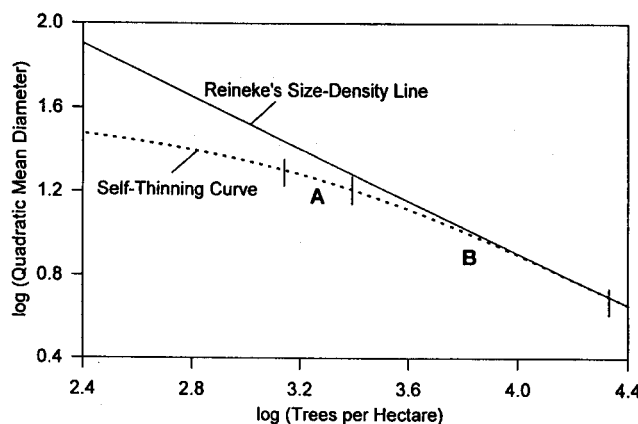
Figure 1. Reineke's (1933) size-density line and the self-thinning curve. Note that the self-thinning curve is approximately linear for either a narrow range of tree densities (interval A), or for a wider range of relatively high tree densities (interval B).

cal models for predicting the development of forest stands will need equations to account for the entire shape of the size–density trajectory. The objective of this study was to produce a more general model of stand development that not only describes the changes in maximum quadratic mean diameter and tree density from stand initiation to self-thinning, but also describes the trajectory of maximum quadratic mean diameter and tree spatial density after self-thinning, where the trajectory departs from Reineke's size–density line.

Data

Data for this study consisted of 615 measurements collected on 147 permanent plots from direct-seeded slash pine (*Pinus elliottii* var. *elliottii* Engelm.) stands on cutover forest sites located in central Louisiana (Natchitoches and Rapides Parishes) and southeast Louisiana (Washington Parish). Some plots were precommercially thinned at age 3 or 4 yr, and none were thinned at older ages. The data were described in detail by Baldwin (1985) and Lohrey (1987). Plot size ranged from 0.040 to 0.048 ha. Stand age varied from 8 to 28 yr, tree density ranged from 445 to 12108 trees/ha, and site index (base age 25 yr) ranged from 9 to 23 m. Each plot was measured from 2 to 6 times, at 3 to 10 yr apart. Figure 2 shows the trajectories of quadratic mean diameter at breast height and tree density for these measurements. A curvilinear relationship between limiting stand diameter and density is evident from the graph.

The data were randomly divided into a fit data set (74 plots) from which regression coefficients were calculated, and a validation data set (73 plots) to evaluate the models. Summary statistics for the fit and validation data sets are
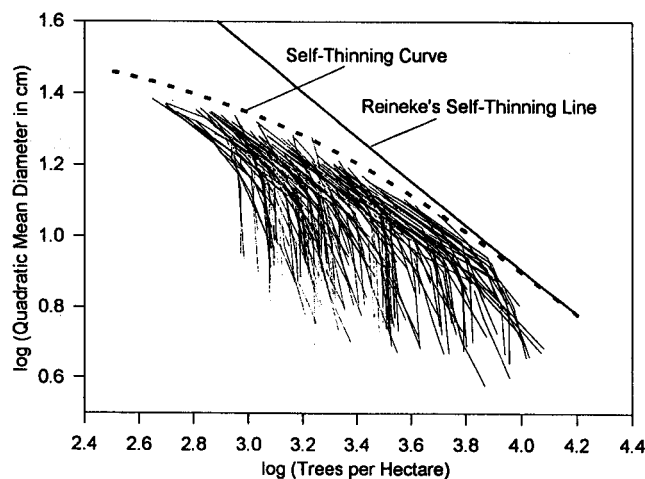

Figure 2. Relationship between quadratic mean diameter at breast height and stand density in direct-seeded slash pine stands. The self-thinning curve is from Equation (4).

presented in Table 1. There were 234 growth measurement periods for either data set.

Model Development

The equations shown below were developed based on the self-thinning rule. The idea was to constrain these equations such that they provided reasonable predictions even when they extrapolated beyond the range of the data. The procedures involved (1) determining a maximum diameter for a given tree density, (2) determining a maximum mortality rate, (3) deriving a tree survival function, and (4) deriving a diameter growth function.

The Maximum Size–Density Curve

Reineke's relationship between quadratic mean diameter (or stand diameter) and tree density [Equation (1)] can be rewritten as

$$Q_r = b_1 N^{b_2}, \qquad (2)$$

where

Q_r = Reineke's maximum stand diameter (in cm),

N = number of trees per hectare, and

b_2 = $1/(-1.605) = -0.623$.

We propose a new relationship:

$$Q_m = Q_r [1 - \exp (b_3 N^{b_4})] \qquad (3)$$

or

$$Q_m = b_1 N^{-0.623} [1 - \exp (b_3 N^{b_4})], \qquad (4)$$

Table 1. Summary statistics for the fit and validation data sets from direct-seeded slash pine stands.

Variable	Fit dataset				Validation dataset			
	N	Mean	Min	Max	*N*	Mean	Min	Max
Age (yr)	308	16	8	28	307	16	8	28
Trees/ha	308	2,694	445	11,861	307	2,827	494	12,108
Basal area (m²/ha)	308	23.79	2.56	52.65	307	23.53	3.28	47.81
Quadratic mean diameter (cm)	308	11.80	3.97	24.30	307	11.83	3.79	23.61
Site index (m) at base age 25 yr	74	18.4	8.5	22.7	73	18.4	8.8	22.9

where Q_m is the maximum stand diameter at tree density N. The value of the expression within the square bracket above ranges from 0 to 1 for negative values of b_3. The values for Q_m and Q_r are similar for large N, but Q_m will gradually break away from Q_r as N decreases. The result is the self-thinning curve shown in Figure 1.

Maximum Mortality

Future tree density at time $i + 1$, N_{i+1}, is limited between two extremes: (a) no mortality, i.e. $N_{i+1} = N_i$, when the stand is far from the self-thinning curve, suffering from little or no competition, and (b) maximum mortality when the stand is near the self-thinning curve, i.e., $N_{i+1} = N_{m, i+1}$, where $N_{m, i+1}$ is the lower limit for stand survival at time $i + 1$ undergoing maximum mortality. This lower limit can be modeled using Pienaar and Shiver's (1981) survival equation:

$$N_{m, i+1} = N_i \exp [b_5 (t_{i+1}^{b_6} - t_i^{b_6})], \qquad (5)$$

where

t_i = stand age in years at time i, and

t_{i+1} = $1 + t_i$.

Survival Function

Future tree density is the weighted average of the two limits mentioned above. The weighting factor, p_N, is between 0 (no mortality) and 1 (maximum mortality):

$$N_{i+1} = (1 - p_N) N_i + p_N N_{m, i+1} \qquad (6)$$

or

$$N_{i+1} = N_i - (N_i - N_{m, i+1}) p_N , \qquad (7)$$

where

p_N = $1 / \{1 + \exp [b_7 t_i + b_8 (Q_{m, i} - Q_i)]\}$,

Q_i = stand diameter at time i, and

$Q_{m, i}$ = maximum stand diameter at time i.

The logistic equation form was used here to constrain predicted values of p_N between 0 and 1. Appropriate respective signs for the coefficients (negative b_7 and positive b_8) assure logical predictions for p_N. For a young stand (small t_i) far from the self-thinning curve (Q_i is very small compared to $Q_{m,i}$), value of p_N is small (little mortality). As the stand matures and approaches the self-thinning curve, p_N increases, resulting in a higher mortality rate. Value of p_N approaches 1 (maximum mortality) for very old stands.

Diameter Growth Function

Diameter growth is constrained such that future stand diameter is bounded by the maximum stand diameter computed from Equation (4) for future stand survival. As the stand grows older, it will approach the self-thinning curve. One way to model this behavior was to let the difference between Q_m and Q_i decrease over time:

$$Q_{m, i+1} - Q_{i+1} = p_Q (Q_{m, i} - Q_i), \qquad (8)$$

or

$$Q_{i+1} = Q_{m, i+1} - p_Q (Q_{m, i} - Q_i), \qquad (9)$$

where

$$P_Q = 1 / [1 + \exp (b_9 t_i^{b_{10}})].$$

A modified form of the logistic equation was used to constrain predicted values of p_Q between 0 and 1. With appropriate respective signs for the coefficients (negative b_9 and positive b_{10}), logical predictions for p_Q are assured. For a young stand (small t_i) the predicted value for p_Q is small, resulting in a large increase in stand diameter.

When a stand reaches the self-thinning curve ($Q_i = Q_{m,i}$), the future stand diameter from Equation (8) is $Q_{i+1} = Q_{m, i+1}$. The stand will follow the self-thinning curve.

Results and Discussion

Fitting Equations

The fit data set was used to estimate parameters in the system of equations developed above (Table 2). Equation (4) to describe maximum stand diameter was fitted to 32 observations that were located near the size–density boundary. Since approximately half of the points were above the resulting curve, and the rest was below the curve, it was necessary to move the curve up vertically so that it was positioned above all data points to represent the limiting boundary curve. This was accomplished by fixing parameter b_1 at 2500 while keeping the parameter estimates for b_3 and b_4 intact.

The equation to predict tree density undergoing maximum mortality [Equation (5)] was fitted to 10% of the data that contained highest annual mortality rates. Since Equations (7) and (9) exhibit the reciprocal effects of stand diameter and density, both equations were fitted simultaneously using SAS procedure MODEL, option SUR (SAS Institute Inc. 1993). The fitting procedure followed the method suggested by Borders (1989).

Evaluations of the Model

The projection ability of the above system of equations was evaluated by applying these equations to all possible growth pairs in the validation data. For example, if a stand was measured at ages 18, 23, and 28, there was a total of three growth pairs: 18–23, 18–28, and 23–28. Box plots of percentage difference for projections of trees per hectare and stand diameter are presented in Figures (3a) and (3b), respectively.

Percent error had a higher standard deviation and larger range for stand density than for stand diameter. Stand density projection was particularly difficult because the size-density trajectories at younger ages varied from near vertical (low mortality rate) for some plots to sloped (higher mortality rate) for others. The projection differences did not exhibit any noticeable trends for both stand density and stand diameter (Figure 3). Good results were obtained from projections up to 11 yr in length. The longer projection lengths (12 yr and above) showed deteriorating results as expected. Overall, accuracy and precision of the projections appeared stable across the projection lengths.

Table 2. Parameter estimates for the system of diameter growth and tree survival equations.

Equation	n	R^2	$S_{y.x}$	Parameter	Estimate	Asymptotic standard error
(4)	32	0.984	0.57	b_1	2,304.53570	103.62430
				b_3	-0.01719	0.00654
				b_4	0.59891	0.06503
(5)	23	0.976	223.31	b_5	-0.19492	0.08216
				b_6	0.86259	0.10920
(7)	234	0.923	452.90	b_7	-0.03606	0.00859
				b_8	0.22151	0.04082
(9)	234	0.956	0.79	b_9	-0.92885	0.43884
				b_{10}	0.37493	0.18449

Final equations:

$$Q_m = 2500 \, N^{-0.623} [1 - \exp(-0.01719 \, N^{0.59891})] \tag{4}$$

$$N_{m,i+1} = N_i \exp[-0.19492 (t_{i+1}^{0.86259} - t_i^{0.86259})] \tag{5}$$

$$N_{i+1} = N_i - (N_i - N_{m,i+1}) / \{1 + \exp[-0.03606 \, t_i + 0.22151 (Q_{m,i} - Q_i)]\} \tag{7}$$

$$Q_{i+1} = Q_{m,i+1} - p_Q (Q_{m,i} - Q_i), \tag{9}$$

where

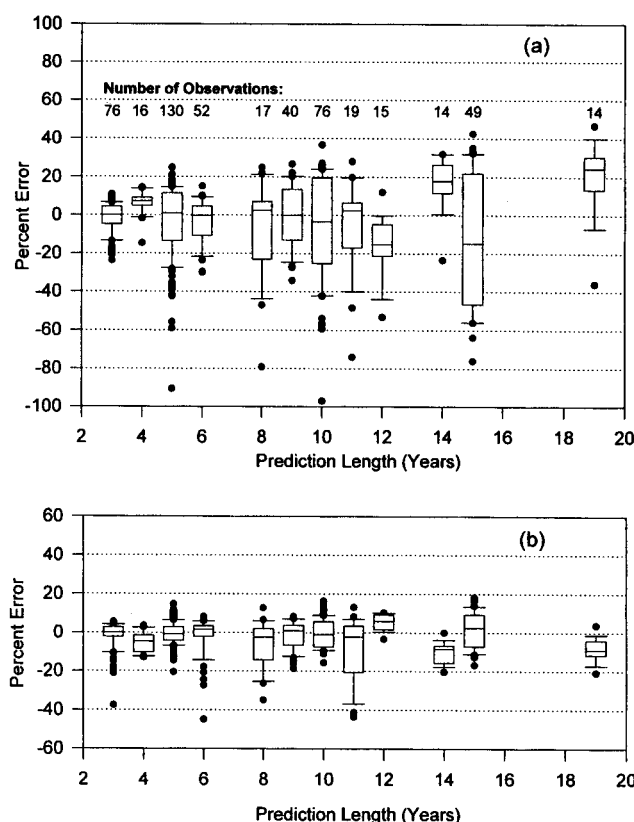$$p_q = 1 / [1 + \exp(-0.92885 \, t_i^{0.37493})]$$

Figure 3. Percent error for projections of (a) trees per hectare, and (b) quadratic mean diameter, applied to all possible growth pairs in the validation data of direct-seeded slash pine stands. The horizontal bars represent the 10th, 25th, 50th, 75th, and 90th percentiles, respectively. The circles represent data outside of the range bounded by the 10th and 90th percentiles. Percent error is defined as 100 (actual–predicted) / actual.

Size–Density Trajectories

Projections of stand diameter and density were performed for five hypothetical stands having initial quadratic mean diameter of 2 cm and initial densities varying from 1,000 to 13,000 trees/ha at age 5. These stands were simulated from age 5 to age 70 (Figure 4). The stands follow vertical trajectories at young ages, indicating that the trees increase their sizes with little mortality from competition. As they grow older, competition sets in, mortality occurs, and the curves start to approach and follow the self-thinning curve.

As the self-thinning curve progressively departs from Reineke's size-density line, stand basal area increases with
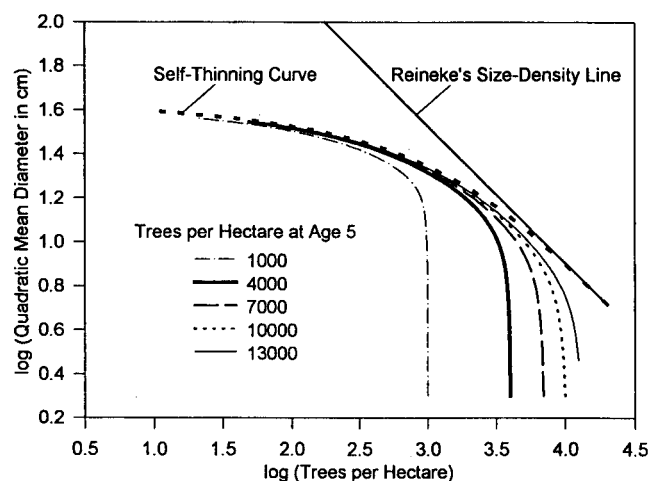

Figure 4. Stand diameter–stand density trajectory from age 5 to age 70 for direct-seeded slash pine stands having initial quadratic mean diameter of 2 cm and initial densities of 1,000, 4,000, 7,000, 10,000, and 13,000 trees/ha at age 5.

age, reaches a maximum and then decreases. This pattern was consistent with trends observed in some empirical growth and yield models for slash pine plantations (e.g., Dell et al. 1979, Zarnoch et al. 1991) and loblolly pine plantations (e.g., Amateis et al. 1984, Baldwin and Feduccia 1987).

Summary and Conclusion

In this article, we assumed that the relationship between quadratic mean diameter and tree density was curvilinear on a log–log scale. Remeasurement data from direct-seeded slash pine stands provided evidence to support this assumption and justify the existence of the self-thinning curve. This curve is very close to Reineke's self-thinning line for high density levels, but it turned away from the self-thinning line as tree density decreased. The slope (or tangent) of the self-thinning curve appeared to be a function of tree density. The value of the slope varied with the range of stand densities in the data. This might explain why researchers reported different slopes of the self-thinning line for the same species.

A system of equations was developed based on the above theory. The self-thinning curve is a collection of maximum attainable stand diameters at various levels of tree density. Future tree density prediction is bounded by a lower limit set by maximum mortality. Diameter growth is also constrained such that future stand diameter is below the maximum stand diameter. The resulting model provided reasonable projections of stand diameter and density of direct-seeded slash pine stands in Louisiana through time. Since the model was constrained according to the self-thinning rule, it should provide reliable predictions for combinations of age, size, and density that occur outside of the range of the current data.

Literature Cited

AMATEIS, R.L., H.E. BURKHART, B.R. KNOEBEL, AND P.T. SPRINZ. 1984. Yields and size class distributions for unthinned loblolly pine plantations on cutover site-prepared lands. Publ. No. FWS-2-84. School of For. Wildl. Res., VPI & SU, Blacksburg, VA. 69 p.

BAILEY, R.L. 1972. Development of unthinned stands of *Pinus radiata* in New Zealand. Ph.D. Thesis, Univ. Ga., Athens. Diss. Abstr. 33/09-B-4061. 73 p.

BALDWIN, JR., V.C. 1985. Survival curves for unthinned and early-thinned direct-seeded slash pine stands. P. 460–465 *in* Proc. of the Third Bienn. South. Silvic. Res. Conf. USDA For. Serv. Gen. Tech. Rep. SO-54.

BALDWIN, JR., V.C., AND D.P. FEDUCCIA. 1987. Loblolly pine growth and yield prediction for managed West Gulf plantations. USDA For. Serv. Res. Pap. SO-236. 27 p.

BORDERS, B.E. 1989. Systems of equations in forest stand modeling. For. Sci. 35:548–556.

CAO, Q.V. 1994. A tree survival equation and diameter growth model for loblolly pine based on the self-thinning rule. J. Appl. Ecol. 31:693–698.

DELL, T.R., D.P. FEDUCCIA, T.E. CAMPBELL, W.F. MANN, JR., AND B.H. POLMER. 1979. Yields of unthinned slash pine plantations on cutover sites in the West Gulf region. USDA For. Serv. Res. Pap. SO-147. 84 p.

DREW, T.J., AND J.W. FLEWELLING. 1977. Some recent Japanese theories of yield-density relationships and their application to Monterey pine plantations. For. Sci. 23:517–534.

HARMS, W.R. 1981. A competition function for tree and stand growth models. P. 179–183 *in* Proc. of the First Bienn. South. Silvic. Res. Conf. USDA For. Serv. Gen. Tech. Rep. SO-34.

LLOYD, F.T., AND W.R. HARMS. 1986. An individual stand growth model for mean plant size based on the rule of self-thinning. Ann. Bot. 57:681–688.

LOHREY, R.E. 1987. Site index curves for direct-seeded slash pines in Louisiana. South. J. Appl. For. 11:15-17.

MACKINNEY, A.L., AND L.E. CHAIKEN. 1935. A method of determining density of loblolly pine stands. USDA For. Serv., Appalachian For. Exp. Sta., Tech. Note 15. 3 p.

MCARDLE, R.E., W.H. MEYER, AND D. BRUCE. 1961. The yield of Douglas-fir in the Pacific Northwest. USDA Tech. Bull. 201 (Rev.). 74 p.

OGAWA, H., K. YODA, AND T. KIRA. 1961. A preliminary survey on the vegetation of Thailand. Nature Life S.E. Asia 1:1–157.

PIENAAR, L., AND B.D. SHIVER. 1981. Survival functions for site-prepared slash pine plantations in the flatwoods of Georgia and northern Florida. South. J. Appl. For. 5:59–62.

REINEKE, L.H. 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46:627–638.

SAS INSTITUTE INC. 1993. SAS/ETS user's guide, version 6, second edition. SAS Institute Inc., Cary, NC. 1,022 p.

SMITH, N.J., AND D.W. HANN. 1984. A new analytical model based on the -3/2 power rule of self-thinning. Can. J. For. Res. 14:605–609.

SMITH, N.J., AND D.W. HANN. 1986. A growth model based on the self-thinning rule. Can. J. For. Res. 16:330–334.

SOMERS, G.L., AND R.M. FARRAR, Jr. 1991. Biomathematical growth equations for natural longleaf pine stands. For. Sci. 37:227–244.

WESTOBY, M. 1984. The self-thinning rule. P. 167-225 *in* Advances in ecological research, Macfadyen, A., and E.D. Ford (eds.). Academic Press, New York.

WHITE, J. 1981. The allomettric interpretation of the self-thinning rule. J. Theor. Biol. 89:475–500.

WILLIAMS, R.A. 1996. Stand density index for loblolly pine plantations in north Louisiana. South. J. Appl. For. 20:110-113.

YODA, K., T. KIRA, H. OGAWA, AND K. HOZUMI. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. J. Biol. Osaka City Univ. 14:107-129.

ZARNOCH, S.J., D.P. FEDUCCIA, V.C. BALDWIN, JR., AND T.R. DELL. 1991. Growth and yield predictions for thinned and unthinned slash pine plantations on cutover sites in the West Gulf region. USDA For. Serv. Res. Pap. SO-264. 33 p.

ZEIDE, B. 1987. Analysis of the 3/2 power law of self-thinning. For. Sci. 33:517–537.